MUTATION CONCEPTS IN RELATION TO ORGANIC STRUCTURE.

THE MUTATION CONCEPT.

SINCE 1900, the idea of discontinuity, perhaps better termed definiteness, in variation, has steadily grown in biological circles. The classical experiments of de Vries on the discontinuous origin of characters in the evening primroses, and of Bateson and the Mendelians on the discontinuous inheritance of characters, has brought much greater definiteness and precision into the thinking on this subject. As a result of the experimental method the different kinds of variation can now be classified, though as yet imperfectly. The type of variation called by de Vries "mutation" has now been studied in many organisms —plants and animals—from bacteria to mammals; and the results of these studies make possible an analysis of the nature of mutation as a natural process.

Of all organisms, the Oenotheras among plants and the pumice fly, Drosophila, among animals, have been most intensively studied from this point of view. In recent years the cytological investigation of the Oenotheras[1] has thrown much light upon the nature of the mutation process, and has been particularly useful in limiting the speculations on

[1] See Gates, "A Study of Reduction in *Oenothera rubrinervis*," *Bot. Gaz.*, XLVI, 1-34, 1908. "Tetraploid Mutants and Chromosome Mechanisms, *Biol. Centralbl.*, XXXIII, 92-99, 113-150, 1913.

Gates and Thomas, "A Cytological Study of *Oenothera* mut. *Lata* and *Oe.* mut. *semilata* in Relation to Mutation," *Quart. Journ. Micro. Sci.*, LIX, 523-571, 1914, etc.

this subject. These cell studies combined with breeding experiments have not only shown that mutation is a phenomenon of variation and not merely of inheritance or hybridization, but they have also thrown considerable light upon the nature of the various changes involved in the origin of different mutants.

These questions have been considered in detail elsewhere,[2] but we may mention here a few of the conclusions regarding the nature of mutations, and a selection of the facts on which these conclusions rest. *Oenothera lata*, one of the mutants from *O. Lamarckiana*, has very characteristic foliage and habit, and is more or less completely male-sterile. This mutant was discovered by de Vries in 1887 and is now known to have constantly 15 instead of 14 chromosomes in its nuclei. This condition arises through one germ cell, when formed, receiving in addition to its normal number (7), a chromosome which does not belong to it. This extra chromosome therefore appears in the fertilized egg and is passed on by mitosis or cell division to every cell in the organism. The mutation is therefore a cell change propagated by mitosis, and the peculiarities of *lata* result from the fact that every nucleus contains an extra chromosome. We shall see that in the same way all the other mutations of *Oenothera* result from different kinds of cell change.

In contrast with *lata*, which arises through an irregular distribution of chromosomes in mitosis, we find in *gigas* a doubling of the whole series of chromosomes, to give an organism having 28 chromosomes in all its cells. The precise manner in which this condition, known as tetraploidy, arises is not yet clear, but a long list of cases of a similar relationship between related species is now known in many genera of plants. Thus we find it among the

[2] *The Mutation Factor in Evolution.* London: Macmillan, 1915. See especially Chapters IX and X.

violets, lady's tresses and cinquefoils, to mention only a few. the tetraploid condition is usually accompanied by gigantism not only of the cells but of the whole plant.

A third and very different type of mutation is found in *O. rubricalyx*, which originated from my cultures of *rubrinervis* in 1907. This mutant differs from its parent only in pigmentation. It is a marked color variety, having deep red buds, with red pigment developed also to a much greater extent in every part of the plant.[3] The offspring of this mutant gave *rubricalyx* and *rubrinervis* in the Mendelian ratio 3: 1. The chromosome-number in *rubricalyx* is unchanged—14, as in *rubrinervis* from which it originated. The origin and hereditary behavior of this mutant may therefore both be explained if we assume that one chromosome of *rubrinervis* has undergone a permanent chemical change so that its presence in the cell leads to greatly increased pigment-production. There is every evidence that this mutation is also a cell change, propagated throughout the developing organism by mitosis, for cells in all parts of *rubricalyx* show an increased content in the anthocyanin pigment.

With these few facts in mind we may now examine briefly some of the points of view which arise.

1. In order to be inherited completely the variation must arise in the nucleus of some cell or cells in the germ track of the organism. Wherever in the life cycle the change originally occurs (and this is usually during the process of chromosome reduction), it will come in the next generation to date from the fertilized egg. As the fertilized egg divides, the variation will be passed on as a *cell-feature* to all parts of the organism.

2. These nuclear changes are, as already observed, of various kinds, some of them essentially morphological,

[3] See Gates, "Studies on the Variability and Heritability of Pigmentation in Oenothera," *Zeitschr. f. Abst. u. Vererbungslehre*, IV, 337-372, 1911.

others essentially chemical. This conclusion is of much importance for evolution, for if correct it means that abundant material is supplied for evolution to have taken place in many directions at once. In this way the divergent and multifarious character of evolution is emphasized.

The Mendelian experimentation with hybrids has crystallized into the presence-absence hypothesis, according to which it is supposed that a recessive character is negative, due to the loss of something from the germ plasm, and a dominant character positive, due to the addition of something. Bateson[4] and others, basing their views of evolution on this hypothesis, have finally narrowed down the evolutionary process to the loss of "factors" or "inhibitors" for factors. This assumes that a single type of germinal change, such as occurs in the origin of *O. rubricalyx,* is the only type of discontinuous variation known. But we have already seen that mutation is a composite process, and that the various kinds of departures from the parent form cannot all be explained on the basis of one idea.

A still more fundamental alteration of the presence-absence hypothesis will be required if the view here expressed be correct. For this view implies that the origin of any pair of Mendelian characters is due, not to the loss or "dropping out" of something from the germ plasm of the organism, giving the negative (recessive) character, but to the sudden modification of the positive (dominant) character to produce the negative, or (in some instances) of the negative character to produce the positive. Thus in the case above mentioned, *O. rubricalyx* has originated from *rubrinervis,* not through the loss of an "inhibitor" from the latter but through a chemical alteration in the germ plasm, or rather in a particular part of it, namely, one chromosome. In the same way we may consider the differ-

[4] Bateson, *Problems of Genetics.* London: Humphrey Milford, 258 pages, 1913.

ence between a round pea and a wrinkled pea to have arisen through an alteration in the chemical nature of one chromosome of the round-pea race, of such nature that, when replacing the unchanged chromosome in the cell, it leads to the production of a race in which the sugar fails to be transformed to starch and the peas are therefore wrinkled. According to this view each new Mendelian character is to be looked upon as the result, not of the loss of something from the cell, but of a *modification* of one part or organ of the cell, or rather of the nucleus.

The conception that each recessive character has resulted from the loss of something from the germ plasm, was very reasonably founded on such cases as that of two white races of sweet pea which when crossed produce in F_1 the purple Sicilian sweet pea, the ancestor of both. It was very reasonable to suppose in such a case that each white race had arisen through the loss of a different "factor" for the production of color, since putting the two together by crossing immediately gave the color. And indeed, so long as no further evidence is available this method of viewing the matter is entirely legitimate and satisfactory.

But if we view each negative character as due to the *modification* rather than the loss of something, at the same time a similar result follows which is more in accord with a sound evolutionary view. Thus in the case of *Oenothera lata* we know that a change which is certainly not a loss, has occurred, yet in the cross *lata* × *nanella,* for example, *Lamarckiana* (the parent of both), as well as *lata* and *nanella,* are produced in F_1. In this instance, since *O. nanella* is a dwarf, it is easiest to think of it as having originated through the loss, or at least the permanent inactivity, of something in the germ plasm. Yet there is probably an equally fundamental sense in which even *nanella* represents a germinal modification rather than a loss,

while in *lata* the loss-conception is excluded. Hence, while the symbols of the presence-absence hypothesis are most useful in dealing with the inheritance of Mendelian characters, yet in order to be strictly accurate we need to modify this terminology when considering the *origin* of these character-differences.

3. We thus arrive at the position that not only is mutation a composite process involving various types of germinal change, but that Mendelian characters also originate in each case through the modification of a particular part of the germ cell. In the phylogeny of organisms we may therefore expect innumerable divergencies, with a number of lines sometimes radiating from the same point. The fact that parallel mutations, i. e., corresponding germinal changes in unrelated lines of phylogeny, frequently take place, increases this radiating tendency.

Aristotle, as is well known, arranged or attempted to arrange all organisms in a single linear series, and it is only in modern times, beginning with Lamarck, that the divergent and radiating nature of phylogenies have been recognized more and more. Herbert Spencer briefly traced the history of thought on this subject in his *Principles of Biology*. Since Spencer's time, as knowledge of the relationships of organisms has grown, this tendency has become still more pronounced, until now biologists recognize that probably never can three living species be arranged in linear series of descent, and paleontologists continually find that forms at first considered in the "direct line of descent" are rather on a longer or shorter "side line" of their own. All this is of course to be expected when we consider that particular elements of the germ plasm vary, each time, and not the germ plasm as a whole. The radiating tendencies must greatly outweigh any tendency to progress in a straight line. Mere divergence is of course to be expected on almost any hypothesis which assumes de-

scent with modification, as was abundantly shown by Darwin in the theory of natural selection. But the mutation conception as I have stated it, in which particular elements of the germ plasm vary independently each time, makes it possible much more easily to account for the prolific radiating tendencies which, according to the consensus of opinion of naturalists, organisms display.

THE EVOLUTIONISM OF BERGSON.

It seems worth while to compare the views of variation and phylogeny resulting from these experimental studies of mutations, with certain views on these matters expressed by Bergson.[5] I am not competent to discuss the fundamentals of Bergson's philosophy, and indeed that is unnecessary, for they have been criticised with admirable lucidity and, as it appears to me, with justice, by Bertrand Russell in this journal.[6] The critic points out, for example, that Bergson's views of number are confused and inconsistent and that number does not necessarily imply space; while Bergson's theory of duration and time rests upon a confusion between "the present occurrence of a recollection and the past occurrence which is recollected," i. e., between the act of knowing and the object known.

Zeno's argument of the arrow Bergson meets by denying that the arrow is ever at any point of its course. He criticizes the mathematical view of change by the statement that it "implies the absurd proposition that movement is made of immobilities." But Russell points out that this absurdity vanishes when it is realized that motion really implies change of relations. Finally the critic considers that when the identification of subject and object which results from Bergson's theory of duration is rejected, his whole system collapses, including the theories of time and

[5] *Creative Evolution.* New York, 1911.
[6] "The Philosophy of Bergson," *Monist*, XXII, 321-347, 1912.

space, his belief in real contingency, and his views that the universe contains only actions and changes but not things.

There are nevertheless certain elements in Bergson's views of evolution in their biological aspects, which appear worthy of consideration. Thus he has clearly recognized and emphasized the nature of the phylogenetic divergence to which I have referred. Life, in his view, is a tendency whose essence is to split up in the course of its development, giving simultaneous divergent or sometimes parallel lines of progress in the form of a sheaf. Such a separation of tendencies led to the plant world which specialized in fixity, insensibility and the accumulation and storage of energy from the sun by means of the chlorophyllian function; and to the animal world with mobility, consciousness, nerve centers and the explosive expenditure of energy in locomotion. All this may be regarded as sufficiently orthodox biology. The questions arise concerning the nature and causes of the diverging tendencies.

Bergson is also doubtless correct in pointing out (p. 135) as a cardinal error of philosophers from Aristotle onward, the idea that vegetative, instinctive and rational life are three successive degrees of development of one tendency. They are rather "three divergent directions of an activity that has split up as it grew," so that the difference is not one of degree but of kind.

Bergson believes that not only have organisms traveled over many diverging roads as an expression of the original *élan vital,* but they have constructed or created the road itself as they traveled; or rather, their own evolution constitutes the road, so that of necessity the road leads to no fixed or predetermined goal such as is implied in a teleological view. We may agree that at the present time science can offer no adequate reason for supposing that the particular directions many phylogenies have taken have been directly determined or narrowly limited by the

conditions on the earth's surface. The distinguishing features of, e. g., mosses, ferns, mammals, echinoderms and mollusks cannot be equated in terms of their different environments; indeed, each of the higher phyla of animals, such as reptiles and mammals, has tended to spread out and occupy all the main types of environment, aerial, terrestrial and aquatic. Nor can we formulate any adequate reason why the characteristic phyla of animals and plants should not, in another evolution under precisely the same earth-conditions, have worked out into quite different end-results. If this is the case, are we justified as biologists in taking the mechanistic attitude that all is given in the original protoplasm, and that the result of evolution has been in this sense a predetermined one? Bergson answers No, that the result has not been narrowly predetermined either in a mechanistic or a teleological sense; and I can see certain reasons for agreeing with him on this point, without at the same time becoming a vitalist. For it is not necessary to take the next step with Bergson, and assume that life is a force or impulse directed against matter and endeavoring to overcome its inertia. The biologist is perhaps more acustomed to think of life as a condition which appears when certain physical and chemical conditions of aggregation have been reached and disappears when the equilibrium of this system is sufficiently disturbed, — a mechanistic point of view.

And now to return to the reasons for agreeing with Bergson that evolution is to some extent, at any rate, indeterminate, so that the history of life on the earth under the conditions which have actually existed might have been different, as regards the characteristics of the various plant and animal phyla, from that which we have witnessed. This, I think, follows from the conclusion reached on a previous page—that particular elements of the germ plasm vary independently. For, this being the case, the *order* of

the occurrence of these variations will be more or less a matter of chance, depending in part on environmental vicissitudes; and each variation, like a move on a chess board, will help to determine by limitation the succeeding variations. If millions of different games can be played with thirty-two chess pieces, no limitation need be placed on the number of organic worlds which might have evolved from the first protoplasm. Nevertheless, if evolution has any meaning we see progress in complexity, and simultaneous development in many phyla as though a number of games were being played through simultaneously to the end without altering the rules of any game during its progress. The irritability of protoplasm and the increase in the organism's control over its environment are, however, rather slender threads on which to hang a completely mechanistic explanation of progressive evolution.

Many biologists will probably agree with Bergson when he says (p. 102), "The truth is that adaptation explains the sinuosities of the movement of evolution, but not its general directions, still less the movement itself." Nor should I dissent from the further statement (p. 101), "Evolution will thus prove to be something entirely different from a series of adaptations to circumstances, as mechanism claims; entirely different also from the realization of a plan of the whole, as maintained by the doctrine of finality. . . . It is one thing to recognize that outer circumstances are forces evolution must reckon with, another to claim that they are the directing causes of evolution." But although we may agree with these statements, we cannot admit the further one that evolution creates, as it goes on, "not only the forms of life, but the ideas that will enable the intellect to understand it." This leads to Bergson's peculiar and complicated philosophic views of the relations between the mind and things—that intellect and matter have progressively adapted themselves to one another in

the course of evolution (p. 204), a conception into which we need not enter.

Before leaving this aspect of the subject we may refer to Bergson's attitude toward the evolutionism of Spencer, which he criticizes as an attempt to reconstruct evolution from fragments of the evolved. His comparison of the Spencerian philosophy of evolution to the thought of a child which may put together the parts of a puzzle picture and in doing so imagine it is creating the design, is a telling argument for Bergson, who points out that the putting together of the fragments has nothing to do with the act of the original artist in producing the design.

We may, therefore, agree with Bergson that one of the great problems of evolution, so great that biologists have scarcely yet acquired the means of beginning a successful attack upon it, concerns the nature and causes of the general currents of animal and plant phylogeny. But his suggestion of an original impulse or *élan vital* impinging upon matter and spreading out into sheafs of organic movement, while a conception most stimulating to thought, is not of a sufficiently explanatory nature to be satisfying to the scientific mind.

VARIATION CONCEPTS IN RELATION TO ONTOGENY.

In his consideration of evolution Bergson naturally adopts attitudes, sometimes implied rather than definitely expressed, toward various questions of variation, heredity and ontogeny, which are worthy of discussion. Like many other writers he selects the eye as an example of a highly adapted organ, and asks how it can have arisen independently in mollusks and vertebrates through purely fortuitous circumstances. In stating the case, however, he is led to make certain assumptions which from our present point of view unnecessarily increase the admittedly great difficulties of any explanation. He says (p. 64): "If the

variations are accidental, how can they ever agree to arise in every part of the organ at the same time, in such way that the organ will continue to perform its function? Darwin quite understood this; it is one of the reasons why he regarded variation as insensible."

But I think we may say that we now know that inherited variations do *not* usually arise independently and simultaneously in different parts of the organism. According to the views of inherited variation already expressed in this paper, the inherited difference is due to a change in the fertilized egg. That change is a *single* thing, although in ontogeny it may work out in variations which express themselves in different parts of the organism and so appear to be independent of each other. Moreover, each inherited change is really a cell change, transmitted as such in plants through all the cells of the organism, and in animals, at least through the cell generations of the germ track. This is therefore the basis of the well-known cases of correlated changes which Bergson aptly characterizes (p. 66) as solidary, for instance the imperfection of the teeth in hairless dogs.

He finds greater difficulties with *complementary* changes, for example in different parts of the eye to improve its function. But these correlations are much less mysterious since the discovery of hormones, which may be produced by one organ and help to regulate the activity of wholly different and structurally remote and independent organs. Still more illuminating in this connection is the manner in which during development one organ is known to influence and even to cause the development of another. Thus it has been shown by Warren Harmon Lewis[7] that when a portion of skin from any part of the tadpole of a frog is grafted over the region where the

[7] Lewis, W. H., "Experimental Studies on the Development of the Eye in Amphibia," *Journ. Exptl. Zoology*, 1905, II, 431-446, pls. 2. Also *Amer. Journ. Anat.*, Vols. III, VI, and VII.

optic vesicle from the brain is developing, the skin of this region will invaginate and form a lens. From these experiments it may be concluded that in normal development the formation of the lens from ectoderm is the result of a stimulus emanating from the optic vesicle. With such facts in mind it is not difficult to understand that many changes apparently complementary and independent are really so interrelated as to be the result of a single change in the germ. The number of ways in which such interrelations can occur, increases the probability of explaining each case of correlated variations as the result of a single original change. This difficulty of Bergson's therefore disappears.

Pursuing the subject further, Bergson asks (p. 65): "How could the same small variations, incalculable in number, have ever occurred in the same order on two independent lines of evolution, if they were purely accidental? And how could they have been preserved by selection and accumulated in both cases, the same in the same order, when each of them, taken separately, was of no use?" The first question we will come to later. With regard to the second the case is overstated, because owing to the correlations of variations mentioned in the last paragraph, a *relatively* short series of evolutionary stages requires to be postulated to account for the evolution of the eye, though it may be admitted that a mere shortening of the series does not remove any of the difficulties. The second question harbors a misapprehension in supposing that the various stages in the perfecting of an organ are in themselves of no service to the organism.

Darwin was at some pains to show that the contrary is really the case. He held that each stage in the evolution of a particular structure was of use to its possessor, although the function of the structure might change completely in the process of development. Thus in the *Origin*

of Species (6th ed., I, 285-290), in answering an objection of Mivart, he suggests a comparison of the condition of the baleen in various whales with that of the palate in members of the duck family. He shows that in the ducks there is a series of stages in the development of the horny plates of the palate, yet each stage is serviceable to the species possessing it, though different species use the structure for different purposes. In conclusion Darwin remarks (p. 289): "Nor is there the least reason to doubt that each step in this scale might have been as serviceable to certain Cetaceans, with the functions of the parts slowly changing during the progress of development, as are the gradations in the beaks of the different existing members of the duck family." The important fact that apparently new organs are often a remoulding and readaptation of organs characteristic of members of a previous phylum or family, is frequently neglected. In such cases, as Darwin points out, the difficulty about the selection of undeveloped rudiments of an organ does not exist because the organ is functioning in every stage although the function changes gradually during the evolution. But the readaptation of organs can never account for their original appearance. This must have taken place in their simplest form, and it has generally been recognized that the fact of mutations or definite variations will help to bridge this difficulty.

Bergson turns next to the hypothesis of sudden variations, to see whether it will solve his problem. He says (p. 65): "It certainly lessens the difficulty on one point, but it makes it much worse on another. If the eye of the mollusk and that of the vertebrate have both been raised to their present form by a relatively small number of sudden leaps, I have less difficulty in understanding the resemblance of the two organs than if the resemblance were due to an incalculable number of infinitesimal resemblances acquired successively; in both cases it is chance that ope-

rates, but in the second case chance is not required to work the miracle it would have to perform in the first. . . . But here there arises another problem, no less formidable, viz., how do all the parts of the visual apparatus, suddenly changed, remain so well coordinated that the eye continues to exercise its function? For the change of one part alone will make vision impossible. . . . The parts must then all change at once, each consulting the others."

But we have already pointed out that the changes *must* be correlated and such as to make development and survival possible, for in order to be inherited they must have arisen in the egg, whence their influence radiates in ontogeny. Germinal changes leading to a less perfectly functional condition of the eye would immediately be eliminated by natural selection. Heredity maintains the species, while it "waits" for another germinal variation which will give the individual an advantage and so lead to the perpetuation of the change and its adoption by the species. The parts concerned do then "all change at once." This is not, however, because each consults the others but because all together are expressions of a germinal change which occurred in the egg. Nor is such a view teleological, because some changes will be advantageous, some innocuous, some bizarre, some harmful; but all unforeseeable even if we knew the nature of the change in the egg, for we at present know practically nothing of the relation between chemical composition and external form in organisms.

Bergson says truly (p. 67) that function is less narrowly bound to form in plants than in animals, a change in leaf-form for example producing no appreciable effect on the function of the leaf. In animals not only is there usually a closer relation between form and function, but there is also, as we have already observed, a greater interaction of organs upon one another through the blood circu-

lation, particularly by means of internal secretions and hormones.

Having briefly considered the subject of accidental variations, and found that Bergson's objections to chance variations as material for evolution are not always well founded, let us return to the subject of parallel evolution, as in the case of the vertebrate and the molluscan eye.

Patten[8] has studied the eyes of Pecten and of other mollusks and arthropods with much care, and we may therefore first examine his results. Some members of nearly all the higher invertebrate groups have relatively highly developed eyes. Thus they are found in many annelid worms and mollusks, and in nearly all Arthropoda. These eyes show a great variety of structure, but may be mainly classed as of three types: (1) the vertebrate type, having a lens; (2) much more commonly, the so-called "compound eye," composed of ommatidia and characteristic of the Arthropoda; and (3) much simpler structures composed essentially of depressed pigment spots. Very often, more than one type of eye occurs in the same individual, and there is no doubt that, as Patten says, "Many complex eyes have originated independently in very limited groups of animals." The same thing is true of various other structures, such as the seed in plants, the seed-habit having developed independently in different plant phyla. We agree with Bergson that the production of such organs represents the expression of a tendency; indeed, this is a frequent scientific form of statement of the facts as observed in phylogenies. The problem which Bergson fully apprehends and seeks to solve is, then, why do we find parallel expressions of the same tendency in independent phyla?

The tendency to form eyes does not appear in all phyla. Thus, so far as I am aware, definite eye structures do not

[8] Patten, Wm., "Eyes of Molluscs and Arthropods," *Mittheilungen zu d. Zool. Station zu Neapel,* VI, 542-756, pls. 28-32, 1886.

occur in any of the Echinodermata. One may think of this fact as indirectly connected with their mode of life, which does not call for highly developed vision. Useless characters which may have appeared through a single fortuitous mutation are to be found in all groups, particularly among plants. But an elaborate mechanism like the eye will only be developed when of sufficient advantage to the organism to have been built up by selection continuing in one direction for many generations. If vision is of no particular advantage to a starfish in its conditions of existence, then there is no "incentive" for the selection of any variations which may occur leading to the formation of organs having increased light-sensibility. Of course the absence of eyes in echinoderms may be due to some other cause, such as the very rudimentary condition of the nervous system, but this is at any rate a possible reason.

One of the remarkable features of the eyes in many mollusks in their great number. Thus, according to Patten, Arca has 250 compound eyes, 800 or 900 invaginated eyes or pigmented pits like those of Patella, and about 200 minute and simple ocelli, making a total of about 1300 eyes. And in addition to these there are numerous small groups of ommatidia. Again, in Pecten there are from 60 to 100 eyes of the highly developed type, while Onchidium and Chiton each have several thousand. In Pecten the eyes on the left mantle are usually arranged in pairs and are larger than those of the right mantle, the latter being spaced at regular intervals on long stalks. This is connected with the fact that the animal rests on its right valve and will turn over if placed on its left. In the young Pecten the ophthalmic fold of the mantle is covered with small pigmented pits like the invaginated eyes of Arca. There are also pigmented papillae containing a few ommatidia, but these later degenerate and disappear. Patten interprets this to mean that the ancestors of Pecten pos-

sessed many invaginated eyes and isolated ommatidia, a condition nearly comparable with that of the present Arca.

The structure of the larger eyes of Pecten is remarkably similar to that of the vertebrate eye. Without going into detail it may be mentioned that there is not only a lens but a cornea and pupil surrounded by a pigmented iris. Focal adjustment of the lens is accomplished (1) by change in shape of the lens, (2) by bodily movement of the lens by means of contractile fibres. It can be shown that a perfect inverted image of any object is thrown by the lens on the rods of the retina, the retina being inverted or reversed in structure as in the vertebrate eye. In certain species of Pecten a number of the eyes have their pupils covered with pigment so they must be functionless, yet they are perfect in structure.

In development, however, as Bergson points out (p. 75), the eye of Pecten differs from the vertebrate eye, in that the whole structure, including both the retina and the lens, is differentiated from an outgrowth from the mantle. Hence the lens does not arise from a separate invagination, and the retina is derived directly from the ectoderm.

Notwithstanding the remarkable efficiency of these molluscan eyes as a mechanism for forming images on the retina, yet the nervous system is in a rudimentary condition and the stimuli are carried to ganglia which cannot properly be considered a brain. In the vertebrates we may (if we choose) think of the image on the retina being transmitted along the optic nerve in the form of differences in nervous stimuli, much as a telephone wire conducts its current. From these stimuli-differences the brain reconstructs the "image" in consciousness. But these eyes in Pecten are evidently developed as image-formers, far beyond the possibility of their use by its simple ganglia. So conspicuous is this over-development that Patten tries to avoid the difficulty by supposing that the primary function of

the eyes in mollusks is to act as heliophags or absorbers of light-energy, while vision is a secondary function of the more highly developed eyes. But I know of no evidence for this view, and it does not seem to have been taken up later. Since the eyes are used in detecting shadows, to which the animal quickly responds, it is probable that this is sufficient to account for their high state of development. Bergson would probably say that the *élan vital* has impelled the organism to form eyes while leaving the nervous system rudimentary, but this is scarcely a causal explanation. On the other hand, one may suppose that natural selection was concerned in the development of these remarkable eyes, for each improvement in the eyes would render the organism better aware of its surroundings (even with an unimproved nervous system) and so aid in its preservation. For some unknown reason, favorable variations leading to great development of the nervous system have not occurred in Mollusca, and hence could not be selected. In the vertebrates on the other hand it is doubtless significant that the optic vesicle originates as a lateral outgrowth from the brain, which later controls the development of the lens. Hence in this case the evolution of the eye and the brain must have gone on together; for according to the view expressed in this paper, each successive germinal variation must have occurred so as to modify the rudiment from which develops both eye and brain. This being the case, as progressive variations successively appeared they would always be coordinated in the two structures, while retrogressive variations, being inefficient, would be eliminated.

Bergson stakes his whole case against mechanism on such instances as this of parallel evolution. Thus he says (p. 54): "Pure mechanism, then, would be refutable, and finality in the strict sense in which we understand it would be demonstrable in a certain aspect, if it could be proved

that life may manufacture the like apparatus by unlike means on divergent lines of evolution." But it is noteworthy that the philosopher and the scientist proceed from opposite ends of the story in approaching a subject of this kind. In discussing, for example, parallel adaptations, the scientist selects a simple case, and having offered an explanation proceeds to apply it to the more difficult ones. But M. Bergson always selects the most difficult and inscrutable instances in making it appear that science cannot solve the problem involved. The simpler cases he passes over entirely.

Thus we know that wings in one form or another have been evolved a number of times independently, as adaptations to aerial flight. The adaptation of a limb for aerial locomotion is a simple change compared with the development of the eye to react efficiently to the extremely delicate wave-motion of light. Yet one cannot but feel, as Darwin felt, that any explanation which applies to the simpler case must also be applicable to the more remote ones. We can understand the modification of fore-limbs into wings through the selection of definite variations which occurred in many directions but were of advantage for flight only when they occurred in one or a few directions. But in the more abstruse case of the eye it is possible to make the facts appear more recondite than they really are. For example, Bergson says (p. 71) regarding the eye: "Certainly the photograph [pigment spot in simple organisms] has been gradually turned into a photographic apparatus [eye]; but could light alone, a physical force, ever have provoked this change, and converted an impression left by it into a machine capable of using it?" In the first place, that the pigment spot is a direct response of the cell to light is an assumption which will require a good deal of proof. But if we consider the simpler case of the wing in flight, it seems absurd to ask, How could the air convert a limb into a struc-

ture capable of using the air in flight? We can realize that the air has not been acting on the limb to produce a wing, and neither need we assume that light acted on a pigment spot to produce an eye. The method has been much more round-about. Conclusions such as this of Bergson's lead us to feel that the solid ground of plodding science is preferable because safer than the more spectacular methods of philosophy.

It appears therefore that although we have not reached a complete understanding of the many cases of parallel evolution, yet the scientific method of attack is the only safe one to follow, for the philosopher's rapid strides constantly lead him into pitfalls.

THE RELATION OF INSTINCTS TO STRUCTURE.

The subject of the variation and development of instinct and intelligence contains several features of interest in this connection. Bergson considers that instinct and intelligence had a common origin, from which they evolved as diverging tendencies, — unlike solutions of the same problem,—culminating on the one hand in the ants and bees and on the other hand in man; the Arthropoda having specialized in instinct while the Vertebrata specialized in intelligence. These two psychic activities or methods of reaction to environment are therefore in a sense complementary and not consecutive stages in any evolutionary series, the most evolved intelligence still retaining something of instinct, and the most advanced instincts something of intelligence.

As in his treatment of parallel evolution, Bergson again singles out a few of the most striking and complex instincts when he comes to consider their origin. He particularly considers (p. 146) the beetle Sitaris which lays its eggs so that the larva will come in contact with the male bee, Anthophora, whence it passes to the female and thence to

one of her eggs where it undergoes a metamorphosis, feeding on the contents of the egg and afterwards on the honey in which the egg floats. The other instinct particularly considered (p. 172) is that of certain Hymenoptera (Ammophila, Scolia, Sphex) which sting their victims in the proper nerve centers to cause paralysis without death, and then store them up as food for the larvae when they hatch. Thus Sphex uses the cricket for this purpose, and stings each victim successively in its three ventral nerve ganglia so as to produce paralysis of movement.

It is, then, Bergson's aim to show that these instincts could not have been evolved by any of the methods proposed by science. He says (p. 169): "These instincts surely could not have attained all at once their present degree of complexity; they have probably evolved; but in a hypothesis like that of the neo-Darwinians the evolution of instinct could have come to pass only by the progressive addition of new pieces which in some way by happy accidents came to fit into the old. Now it is evident that in most cases instinct could not have perfected itself by simple accretion; each new piece really requires, if it is not to be spoiled, a complete recasting of the whole." And then he asks triumphantly, "How could mere chance work a recasting of the whole?"

But this all implies a mistaken conception of the relation of variation to ontogeny. The real variation, as we have already emphasized, in order to be inherited must arise in the germ cells, or the fertilized egg; and hence any variation, before it comes into expression, must have had an ontogenetic development which is a part of the ontogeny of the whole organism. Modification of an instinct, as of any other feature, through a variation, therefore means that *every ontogenetic stage is modified* and that the whole is necessarily to some extent recast. This reasoning applies most clearly to structural variations,

but the same reasoning must be true in its application to variations in instincts. If such variations have a structural basis at all (and how else can we think of them?) they must result from the unfolding of variations which occurred in the egg. Hence it is reversing the course of events to think of successive variations as "new pieces" which by "happy accidents" come to fit into the old. No such happy accident is required or indeed possible, for every variation-stage of each structure or instinct must be not only compatible with development but also with survival and inheritance, until a new variation (which is subject to the same limitations) again modifies not only the end-stage but the whole series of stages of ontogeny.

It should be pointed out that the same reasoning applies when species are modified through inheritance of acquired characters. For in this conception also the germ cells are modified and the modification expresses itself in the variation of the adult offspring; the only difference being that the neo-Lamarckian doctrine postulates the variation of the germ as resulting from the reflection of environmental effects from the soma back into the germ cells. In either case the modification of the germ cells expresses itself in a modified ontogeny and adult stage; but in one case the variation originated in the egg or sperm from unknown causes, while in the other it originates in the soma from stress of the environment, and secondarily affects the germ cells. The cases of what is known as parallel induction, in which the organism is environmentally modified in its ontogeny by new conditions, and at the same time its germ cells are so altered as to produce the modified type even under ordinary conditions,[9] are in harmony with these views.

Bergson goes on to say (p. 169): "I agree that an acci-

[9] Cf. W. E. Agar, "Transmission of Environmental Effects from Parent to Offspring in *Simocephalus vetulus*," *Phil. Trans. Roy. Soc.*, B, 1913, CCIII, 319-350, Fig. 5.

dental modification of the germ may be passed on hereditarily, and may somehow wait for fresh accidental modifications to come and complicate it. I agree also that natural selection may eliminate all those of the more complicated forms of instinct that are not fit to survive. Still, in order that the life of the instinct may evolve, complications fit to survive have to be produced. Now they will be produced only if, in certain cases, the addition of a new element brings about the correlative change of all the old elements. *No one will maintain that chance could perform such a miracle* (my italics); in one form or another we shall appeal to intelligence."

But we have already seen that an inherited variation *must* cause just such correlative changes. They cannot be avoided. This we regard as the teaching both of embryology and cytology in plants and animals. And if this happens with regard to structure we cannot see any reason why it should not happen in the evolution of instincts. Bergson here again raises difficulties which are really nonexistent; but in this he has followed many biologists who have held a similar view. But if the view I have expressed be correct (and it appears to be the inevitable conclusion of the more recent cytological work in embryology and mutation), then the problem of adaptation is vastly simplified. It is no longer necessary to call in intelligence, as Bergson does, to account for the fact that "the addition of a new element" brings about the correlative modification of all the old elements. That is the natural and essential way in which all variations, whether in structure or instinct, become incorporated into the species.

The comparative study of instincts makes it clear that modifications in instinct and in structure go together, and it seems reasonable to suppose that such correlated variations result from a change in the structure of the egg. If this is the case, the need for an "effort" on the part of

the species, as Bergson suggests, to modify its instinct, is dispensed with. This idea of Bergson's is Lamarckism at its weakest.

It is no doubt a matter of great difficulty, if not impossibility, to conceive how certain instincts can be inherited, and therefore transmitted through the structure of the egg; e. g., the instincts already mentioned of the Hymenoptera which carefully sting their prey in the necessary spots to cause paralysis without death. But is the transmission of such an instinct through the structure of the egg any more difficult to conceive than the inheritance of intellectual differences in man, which we know to take place? If the instinct, like the structure, of the adult insect is implicit in the egg, then it is not necessary to invoke the inheritance of acquired characters, as does Bergson, to account for the origin and inheritance of instincts. The fact that instincts are variable does not militate against this view, for so are structures. May we not thus conceive of instincts developed stage by stage without stating them in terms of intelligence, though they are inherited, just as intelligence is inherited? This does not, however, help us to understand how instinct and intelligence are implicit in the structure of the egg.

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